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Muscle Activity in Steady Swimming Scup, *Stenotomus chrysops*, Varies With Fiber Type and Body Position

DAVID J. COUGHLIN[1] AND LAWRENCE C. ROME[2]

[1]*Science Division, Widener University, One University Place, Chester, Pennsylvania 19013; and*
[2]*University of Pennsylvania, Department of Biology, Leidy Laboratory, Philadelphia, Pennsylvania, 19104, and Coastal Research Laboratory, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543*

Abstract. The red and pink aerobic muscle fibers are used to power steady swimming in fishes. We examined red and pink muscle recruitment and function during swimming in scup, *Stenotomus chrysops*, through electromyography and high-speed ciné. Computer analysis of electromyograms (EMGs) allowed determination of initial speed of muscle recruitment and duty cycle and phase of muscle electromyographic activity for both fiber types. This analysis was carried out for three longitudinal positions over a range of swimming speeds. Fiber type and longitudinal position both affected swimming speed of initial recruitment. Posterior muscle is recruited at the lowest swimming speed, whereas more anterior muscle is not initially recruited until higher speeds. At more anterior positions, the initial recruitment of pink muscle occurs at a higher swimming speed than the recruitment of red muscle. The duty cycle of pink muscle EMG activity is significantly shorter than that of red muscle, reflecting a difference in the onset time of activation during each cycle of length change: pink muscle onset time follows that of red. The different patterns of usage of red and pink muscle reflect differences in their contraction kinetics. Because pink muscle generates force more rapidly than red muscle, it can be activated later in each tailbeat cycle. Pink muscle is used to augment red muscle power production at higher swimming speeds, allowing a higher aerobically based steady swimming speed than that possible by red muscle alone.

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Email: coughlin@popt.science.widener.edu

Introduction

Steady swimming in teleosts is powered by aerobic muscle fibers (Rome *et al.*, 1984; Bone, 1989), including the slow-twitch red muscle and the intermediate-twitch pink muscle (Coughlin and Rome, 1996). These muscle fibers are arranged in relatively thin longitudinal bands, with the pink muscle medial to the red muscle. During steady swimming, red muscle is used at the lowest swimming speeds (Rome *et al.*, 1984). Pink muscle reportedly is not recruited until intermediate swimming speeds (Johnston *et al.*, 1977). At the maximum steady swimming speed, both red and pink muscle are recruited (Coughlin and Rome, 1996).

Muscle function and power production in a steadily swimming fish have recently been detailed for scup (Rome *et al.*, 1993; Coughlin and Rome, 1996; Coughlin *et al.*, 1996). These studies have employed the workloop technique (Josephson, 1985) to examine power production by isolated muscle bundles activated using patterns of muscle length change and muscle stimulation that had been recorded *in vivo* from swimming fish. At the maximum steady swimming speed (the highest speed before white muscle recruitment), scup generate most of the power for swimming by using the aerobic muscle fibers of the posterior myotomes (Rome *et al.*, 1993; Coughlin and Rome, 1996).

Coughlin *et al.* (1996) found several differences between the contraction kinetics of red and pink muscle. First, pink muscle has faster kinetics than red muscle. In isometric contractions, the rates of activation and relaxation of pink muscle are about twice those of red muscle. These rates will influence power production by each muscle type, and therefore, they may affect how the muscle is recruited and activated in a swimming fish. During oscillatory activity such as swimming, muscle must alternately be activated and

relax during each tailbeat cycle. The muscle is activated to generate force during shortening and must relax at the end of shortening to minimize the "negative" work done on the muscle to lengthen it. For most fish muscle, activation occurs during the lengthening phase, giving the muscle time to generate force so that force peaks as shortening begins. Because pink muscle activates more quickly than red muscle, the onset of pink muscle stimulation can lag behind that of red muscle during each cycle of length change, as we have previously found at maximal swimming speeds (Coughlin and Rome, 1996). This appeared to help minimize the negative work that is due to a high force level at the end of lengthening. Finally, because the offset of red and pink muscle electromyographic activity during each cycle of length change occurs at the same time, this also resulted in the EMG duty cycle of pink being less than that of red muscle at the highest aerobic swimming speed. In this study, we analyze whether these patterns of recruitment occur at submaximal steady swimming speeds as well.

Under optimized conditions of oscillatory activity and at oscillation frequencies greater than 4 Hz, pink muscle produces more mass-specific power than red muscle. However, at low frequencies of oscillation, isolated scup pink muscle shows a marked reduction in power production compared to red muscle. In workloop experiments at oscillation frequencies below 4 Hz, force levels drop rapidly in pink muscle during the shortening phase of each length change. The mechanistic reasons for this drop in force during shortening at low frequencies are not known (Coughlin *et al.*, 1996), but this observation leads to a prediction that pink muscle should not be recruited at low swimming speeds that correspond to relatively low tailbeat frequencies.

In this study, we used electromyography to record the activity of red, pink, and white muscle in swimming scup over a range of steady swimming speeds. We examined the effects of swimming speed, longitudinal position on the fish, and fiber type on muscle electromyographic activity parameters such as swimming speed of initial recruitment, relative phase of red and pink muscle activation, and duration of electromyographic activity. Also, for a limited number of swimming speeds, the phase of EMG relative to the cycle of length change could be determined. Data collected permit an analysis of how pink and red muscle are used during steady swimming in scup over a range of speeds.

Materials and Methods

Scup, collected in June 1994 at Cape Cod, Massachusetts (n = 12, length ± SD = 21.8 ± 1.4 cm), swam in a recirculating water treadmill (Rome *et al.*, 1990). Electromyograms (EMGs) were recorded from fish swimming at speeds ranging from 1.5 to 3 body lengths (BL) per second at 10°C (~30 to 60 cm s^{-1}) and from 2.5 to 4.25 BL per second at 20°C (~50–85 cm s^{-1}). These are the ranges of steady, aerobic swimming speeds exhibited by these fish. For each temperature, the fish would not reliably swim at lower speeds, and swimming at higher speeds was "unsteady," indicating anaerobic activity due to the recruitment of white muscle.

For each fish, EMGs were recorded simultaneously from red and pink muscle at one of three longitudinal positions along the fish: the ANT-1, ANT-2, and MID positions, which are defined as 28%, 40%, and 55% of the total length from the anterior tip or snout (Rome *et al.*, 1993). Recordings were not made in the POST position (70%), because this position had no distinct layer of pink muscle (Zhang *et al.*, 1996). When possible, recordings were made from two positions simultaneously (Table 1). In addition, white muscle recordings were made at the ANT-2 position in all fish. The recording technique has been previously detailed (Rome *et al.*, 1990, 1992). Fish were anesthetized with tricaine methanosulfate (MS-222) at a dosage of 50 mg l^{-1}. They were maintained during the surgical procedure with regulated respiratory current pumped across their gills. A hypodermic needle was used to insert twisted wire (Teflon-coated Medwire) bipolar electrodes into the muscle. All wires were sutured at their point of entry and collectively near the back of the dorsal fin. Fish recovered quickly from anesthesia when returned to the holding tank. Fish were swum 24 h after surgery at either 10° or 20°C. Fish swum at two temperatures were allowed to adjust to a change of temperature for 48 h. Grass amplifiers filtered the electromyographic signal with a bandwidth of 10 to 3000 Hz and a 60-Hz notch filter. The placement of electrodes into either

Table I

Specimens and conditions used for electromyographic recordings of the swimming musculature of scup

Fish number	Total length (cm)	Aerobic fiber position	Temperature (°C)
2	23.1	ANT-1	20
4	21.0	ANT-2, MID	20
7	22.2	ANT-2, MID	20
8	23.2	ANT-2	20
9	20.3	ANT-1	20
10	22.0	ANT-1, ANT-2	20
11	21.1	ANT-1, MID	20
19	23.7	ANT-2, MID	10, 20
20	23.6	ANT-2, MID	10, 20
22	19.7	ANT-1, ANT-2	10, 20
24	20.5	ANT-2, MID	10
25	21.0	ANT-1, ANT-2	10

For all fish, white muscle activity was recorded at ANT-2. For each fish, the aerobic muscle fibers (red and pink) were recorded at one or two positions for one or two temperatures. For each position and fiber type, electromyographic activity was analyzed for a minimum of four tailbeat cycles.

the thin pink layer or the overlying red muscle was verified through dissection after each experiment. Also, the nature of the signal indicated that cross-talk between red and pink muscle recordings was not occurring. The pink and red muscle EMG waveforms at one position were not the same.

The EMGs from swimming fish were analyzed using custom macros in DATAPAC software. The semi-automated analysis of the EMG computer files permitted characterization of bursts of electromyographic activity. For each muscle fiber type at each longitudinal position, several variables relating to muscle activity were measured at each swimming speed. First, swimming speed of initial recruitment, or the minimum speed at which bursts of activity could be detected, was determined for each fiber type at each position. Bursts were identified by an algorithm that examined the first derivative at each point in a rectified EMG trace. For each rectified trace, a threshold was set to distinguish the slowly varying background noise from the spikes of electromyographic activity. Spikes were identified as points in the trace that exceeded this threshold, and each burst was then identified as a string of consecutive spikes.

Burst duration, or the length of each electromyographic burst, was expressed as duty cycle, the duration of muscle activity as a proportion of the period of tailbeat oscillation. The relative timing of the onset of activity in red and pink muscle in each tailbeat cycle was also analyzed. The phase difference between the times of activity onset in red and pink muscle was determined for each fish at each longitudinal position for each swimming speed. Phase difference was expressed as a proportion of the oscillation period. Positive values indicate that the activity of red muscle occurred before that of pink muscle; negative values indicate that pink muscle activity had an earlier onset.

For swimming at 2.5 and 4.0 BL s^{-1} at 20°C, patterns of muscle length change were also determined. The fish were filmed from above with high-speed ciné. The films were synchronized with the EMG traces (Rome, 1995). Body curvature and the associated muscle length change characteristics, including the amplitude and frequency of muscle oscillation, were then determined from the films (Rome *et al.*, 1992, 1993; Coughlin and Rome, 1996). For these swimming bouts, the relative phase of the electromyographic activity with respect to the muscle length change was calculated for both fiber types. Phase was defined as the timing of the electrical activity with respect to the beginning of muscle shortening (maximum length) and was determined separately for red and pink muscle as previously reported (Coughlin and Rome, 1996). The phase was expressed as a proportion of the period of tailbeat oscillation and is similar to the On-β shift reported by Jayne and Lauder (1995, 1996).

Results

As swimming speed increased, so did tailbeat frequency (Fig. 1). For swimming at both 10° and 20°C, the increase of tailbeat frequency with swimming speed is well fit by a linear regression for the range of steady swimming speeds. The swimming speed at which initial muscle recruitment occurred varied significantly with both muscle fiber type and longitudinal position (Table II). At 20°C, muscle from more posterior positions was recruited at a lower swimming speed than muscle from anterior positions. At the MID position, red muscle and pink muscle were initially recruited at the lowest steady swimming speed, 2.5 BL s^{-1} (Fig. 2). At the ANT-2 position, red muscle was also recruited at the lowest steady swimming speed, but pink muscle was not recruited until at least 3.0 BL s^{-1}, and not until 4.0 BL s^{-1} in some fish (Fig. 2). At the ANT-1 position, red muscle was initially recruited at 2.5-3.0 BL s^{-1}, whereas pink muscle was not initially recruited until an average of almost 4 BL s^{-1}. Similar trends hold for 10°C. Both red muscle and pink muscle at the MID position were initially recruited at the lowest steady swimming speed, 1.5 BL s^{-1} (Fig. 3). At the ANT-2 position red muscle was also recruited at this speed, but the swimming speed of initial recruitment for pink muscle was significantly faster (1.9 BL s^{-1}, $t = 3.67$, $P = 0.021$ with $df = 4$, Fig. 3). At the ANT-1 position, sample size was limited ($n = 2$). In these fish, red

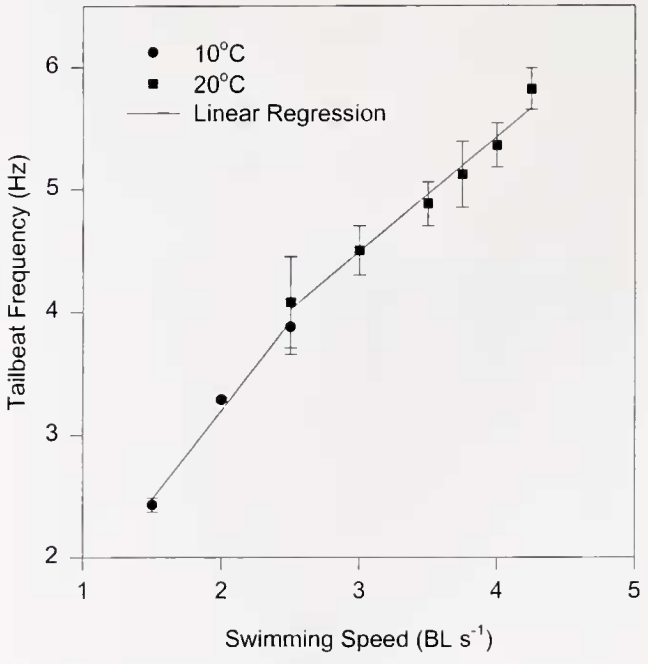

Figure 1. Tailbeat frequency as a function of swimming speed at two temperatures. The regression equations are as follows: tailbeat frequency = 0.30 + 1.45 (swim speed), $r^2 = 0.99$ and $P = 0.012$ at 10°C; and tailbeat frequency = 1.679 + 0.938 (swim speed), $r^2 = 0.97$ and $P < 0.001$ at 20°C.

Table II

Swimming speed (in body lengths per second ± SE) at which aerobic muscle in swimming scup is initially recruited varies with both fiber type and longitudinal position

	Longitudinal Position			
Fiber type	ANT-1 (n = 5)	ANT-2 (n = 7)	MID (n = 5)	POST (n = 5)
Pink	3.8 ± 0.1	3.3 ± 0.2	2.6 ± 0.1	—
Red	2.7 ± 0.1	2.5 ± 0.0	2.5 ± 0.0	2.5 ± 0.0*

Initial recruitment speeds were determined at 20°C through automated analysis of EMG bursts; the recruitment speed for a given position and fiber type is the minimum speed at which bursts were detected. Sample size (n) is given for each position. Longitudinal position (F = 15.4, $P < 0.001$) and fiber type (F = 48.9, $P < 0.001$) both had an effect on recruitment speed. There was also an interactive effect (longitudinal position × fiber type; F = 8.3, P = 0.001).

* There is no identifiable pink muscle layer at the POST position, just a scattered distribution of pink muscle fibers within the red muscle layer (Zhang *et al.*, 1996). The value given for red muscle represents unpublished data.

muscle was initially recruited at 2.0 BL s^{-1}, and pink muscle was not recruited until 2.25 BL s^{-1}. White muscle recruitment (at the ANT-2 position) was observed in all fish at a speed of 4.5 BL s^{-1} at 20°C and at a speed of 3.0 BL s^{-1} at 10°C.

The stimulation of red muscle during each tailbeat cycle occurred at the same time as or just prior to stimulation of pink muscle for most swimming conditions at 20°C (Fig. 4, Table III). Phase difference (red *vs.* pink) was positive for all three positions at 4 BL s^{-1}. This was true for the MID position at all swimming speeds. However, at lower swimming speeds, the time of electromyographic activity onset for pink and red muscle was the same for the more anterior positions; that is, the phase difference of red and pink muscle was near zero (Fig. 4). Swimming speed and longitudinal position significantly affected the onset time for red *vs.* pink muscle during each tailbeat cycle (two-way ANOVA: for swimming speed, F = 3.484, P = 0.009; for longitudinal position, F = 3.640, P = 0.028). Pink muscle and red muscle are both activated prior to the beginning of shortening during each cycle of length change (Table III). The onset time for red muscle is before that of pink muscle, as described above. The phases of red and pink muscle are closest to one another at anterior positions and at lower swimming speeds. Generally similar results were obtained for swimming at 10°C, but sample sizes were limited at that temperature.

The duty cycle of muscle activity during swimming at 20°C was affected significantly by fiber type (F = 4.34, P = 0.04; Table III). Red muscle had longer duty cycles than pink muscle. When data from the POST position are included, duty cycle was significantly affected by longitudinal position (F = 12.571, $P < 0.001$). This agrees with many other studies, such as Jayne and Lauder (1995) on bass, Wardle and Videler (1993) for both mackerel and saithe, and Rome *et al.* (1993) for scup red muscle.

Discussion

The recruitment and activity of aerobic swimming muscle depends on several variables: the type of muscle fiber, the longitudinal position on the fish, and the swimming speed. Pink muscle, with its faster kinetics, is used differently than red muscle. Whereas red muscle is active at most positions at all swimming speeds, pink muscle activity is restricted on the basis of both longitudinal position and swimming speed.

Swimming speed of initial recruitment and duty cycle

Fiber type affects the patterns of recruitment during swimming. Initial recruitment of pink muscle occurs at swimming speeds the same as or higher than recruitment speed of red muscle for all longitudinal positions. Pink muscle recruitment occurs at the lowest swimming speeds for the MID position only; at other positions, pink muscle is initially recruited at higher speeds than red muscle. Pink muscle is used minimally at low swimming speeds, when the tailbeat frequency and the frequency of oscillation of muscle are lowest. This correlates with the low power output of pink muscle at low oscillation frequencies.

Aerobic muscle recruitment is also affected by longitudinal position on the fish. Positions more posterior on the fish body are recruited before anterior ones, particularly for pink muscle. Although pink muscle generally is recruited at the lowest steady swimming speed at the MID position, it is not recruited until higher swimming speeds at more anterior positions. At ANT-1, pink muscle is not consistently recruited until the near-maximum steady swimming speed. The pattern is less obvious for red muscle. At the lowest steady swimming speed, red muscle was active at the POST (Rome, unpubl. data), MID, and ANT-2 positions. At ANT-1, red muscle was not always recruited at the minimum steady swimming speed. This pattern makes sense from a functional viewpoint. ANT-1 pink muscle and red muscle undergo very low strain during swimming, even when the muscle is recruited. For instance, although all aerobic muscle fibers are recruited at 4.0 BL s^{-1} in scup, red muscle strain is around ±2.0% for the ANT-1 position (Rome *et al.*, 1993), and red and pink muscle strain at the ANT-2 position is less than ±3% (Table III). At low swimming speeds, the combination of low strain and low oscillation frequency limits power production by the aerobic muscle (Coughlin and Rome, 1996). Power output of cyclically active muscle is a function of work per cycle and cycle frequency. If work per cycle is limited by very low muscle strain and if cycle frequency is low, power output will be low as well. In scup, the anterior aerobic musculature (pink

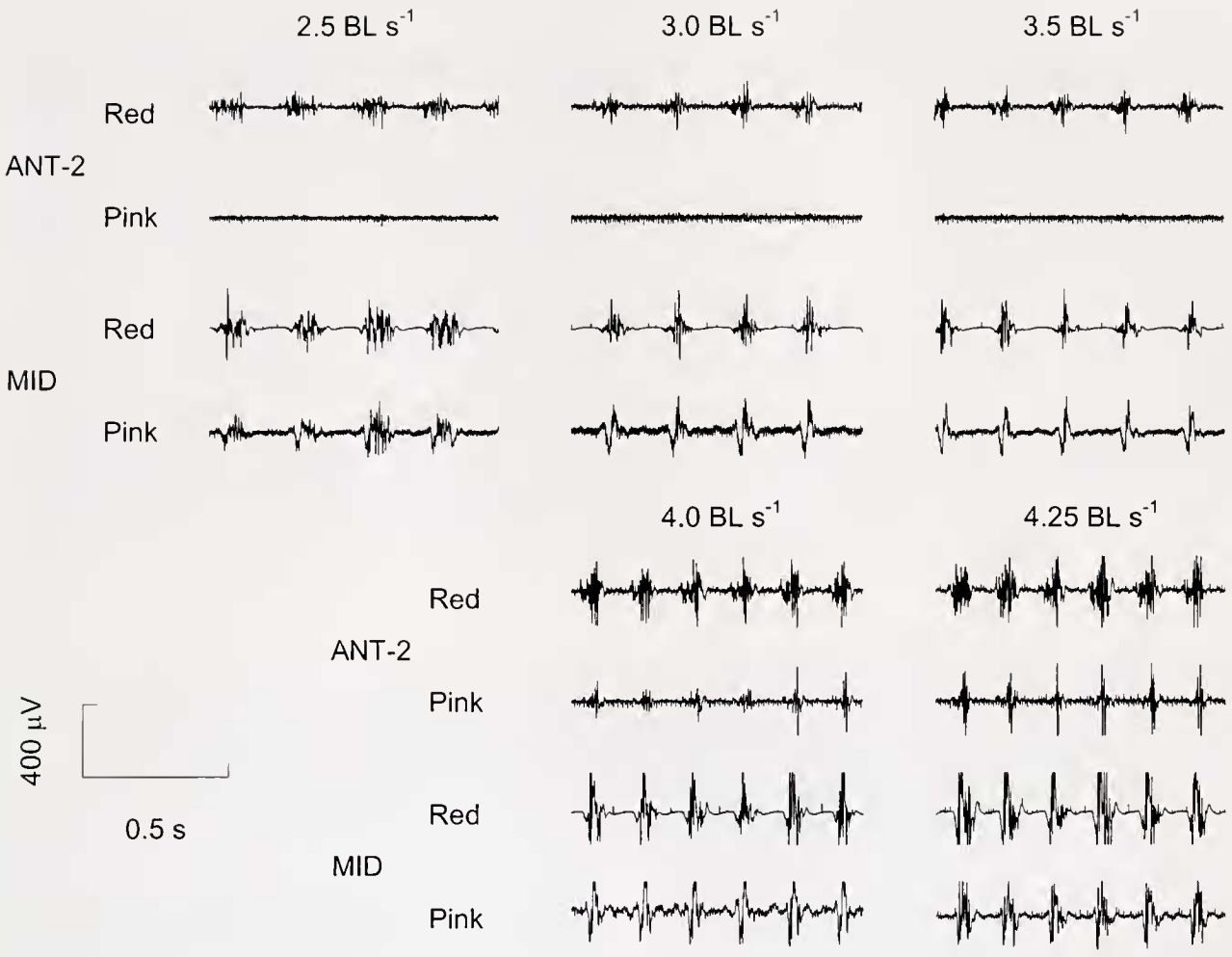

Figure 2. Electromyograms from red (R) and pink (P) muscle at the ANT-2 and MID positions for a scup swimming at 20°C. Each trace is 1.0 s long. BL = body length. In this fish, both red and pink muscle are recruited at a swimming speed of 2.5 BL s^{-1} at the MID position. Red muscle at the ANT-2 position is recruited at this speed as well, although pink muscle at the ANT-2 position is not recruited until 4.0 BL s^{-1} (as determined by computer-driven burst analysis).

and, to a lesser extent, red muscle) is not consistently recruited at low swimming speeds when power production would be low or negative.

A recent report on muscle function in swimming eels (Gillis, 1998) describes a pattern of recruitment for red muscle similar to that in scup. Posterior red muscle is recruited at the lowest steady swimming speeds, and red muscle from more anterior positions is initially recruited at higher steady swimming speeds.

The results presented here for recruitment of red, pink, and white muscle in scup agree in a general sense with the work of Johnston and colleagues. Johnston *et al.* (1977) reported that pink muscle recruitment occurs at swimming speeds intermediate between those of red and white muscle. This seems to be due to the intermediate kinetics of pink muscle relative to the slower red and the faster white muscle (Coughlin *et al.*, 1996). In scup, the initial speed of pink muscle recruitment is most clearly intermediate at the ANT-2 position (Table II). At the MID position, recruitment of red and pink muscle occurs at the same swimming speed. At the ANT-1 position, pink muscle is often not recruited until the maximum steady swimming speed, just before recruitment of white muscle. That red and pink muscle at one longitudinal position can be recruited to power swimming independently raises an interesting question about the innervation patterns of the aerobic swimming musculature.

Fiber type has a significant effect on duty cycle. For most swimming speeds and at most positions, the duty cycle of red muscle is longer than that of pink muscle. The simultaneous offset of electromyographic activity for red and pink fibers in scup holds true across the range of swimming speeds reported here. Interestingly, the approximately simultaneous offset of all red muscle on one side of the fish has been observed in a number of fish species, such as scup

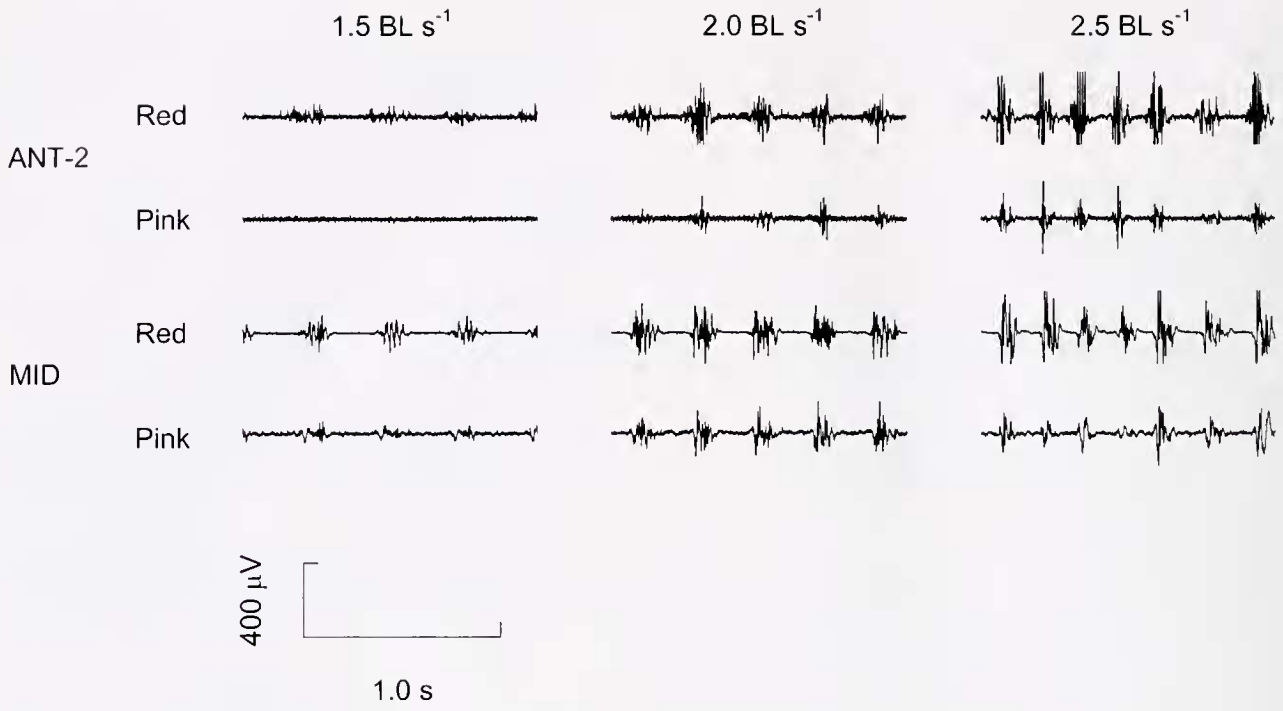

Figure 3. Electromyograms from red (R) and pink (P) muscle at the ANT-2 and MID positions for a scup swimming at 10°C. Each trace is 1.5 s long. BL = body length. In this fish, both pink and red muscle are recruited at a swimming speed of 1.5 BL s^{-1} at the MID position, although pink muscle recruitment is relatively weak. At the ANT-2 position, red muscle is weakly recruited at 1.5 BL s^{-1}, but pink muscle is not recruited until 2.0 BL s^{-1} (as determined by computer-driven burst analysis).

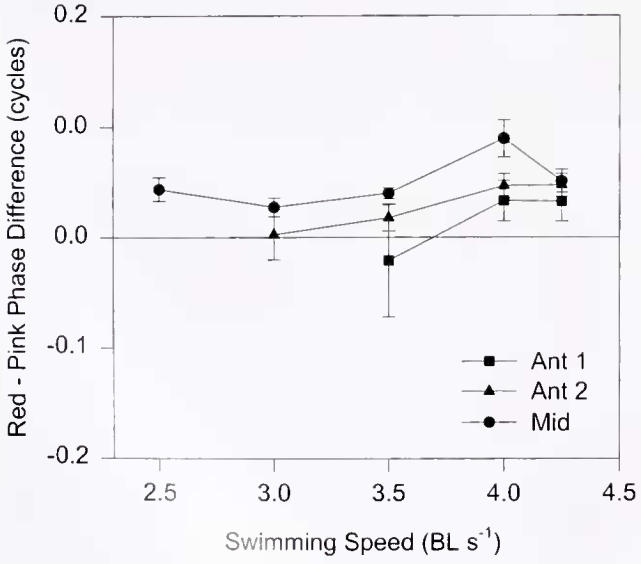

Figure 4. Phase difference of red and pink muscle for three longitudinal positions across the range of steady swimming speeds at 20°C. The difference in the timing of onset electromyographic activity in red and pink muscle during each length change cycle is expressed as a proportion of the period of one cycle. Positive values of relative phase indicated that red muscle is stimulated before pink muscle during each length change cycle.

(Rome *et al.*, 1993; Coughlin and Rome, 1996), carp (van Leeuwen *et al.*, 1990), bass (Jayne and Lauder, 1995), and mackerel and saithe (Wardle and Videler, 1993). Alternatively, more elongate fish that swim with greater body curvature do not have a simultaneous offset of the red muscle electromyographic activity. Instead, the offset of red muscle activation progresses from anterior to posterior, just as the wave of the onset of activation progresses (Wardle *et al.*, 1995; Hammond *et al.*, 1998). Not enough is known about the nervous control of swimming muscle activity to explain the variety of aerobic fiber activation patterns seen in swimming fish.

Phase of muscle activity

Both red muscle and pink muscle are activated prior to muscle shortening for most swimming conditions, such that there is a negative phase shift of electromyographic activity relative to shortening. This agrees with most previous work on red muscle in steady swimming fish such as bass (Jayne and Lauder, 1995, 1996), mackerel and saithe (Wardle and Videler, 1993), carp (van Leeuwen *et al.*, 1990; van Leeuwen, 1995), eel (Williams *et al.*, 1989; Wardle *et al.*, 1995), adult rainbow trout (Hammond *et al.*, 1998), and with previous work on scup (Rome *et al.*, 1993). All of these

Table III

Patterns of in vivo *muscle activity for scup swimming at 2.5 and 4 BL* s^{-1} *at 20°C with a tailbeat frequency of 4.0 and 6.0 Hz, respectively*

		2.5 BL s^{-1}		4.0 BL s^{-1}	
	Fiber type	ANT-2 (n = 4)	MID (n = 3)	ANT-2 (n = 9)	MID (n = 4)
Strain	Pink	3.69 ± 0.31	4.06 ± 0.20	2.62*	3.43*
	Red	3.6*	5.5*	2.9*	4.8*
Duty cycle	Pink	0.310 ± 0.062	0.367 ± 0.021	0.412 ± 0.021	0.331 ± 0.037
	Red	0.395 ± 0.040	0.403 ± 0.040	0.421 ± 0.016	0.391 ± 0.014
Phase	Pink	−14.5 ± 11.4	−52.1 ± 26.4	−14.5*	−17.6*
		(−0.040)	(−0.145)	(−0.040)	(−0.049)
	Red	−16.1 ± 20.7	−65.2 ± 27.7	−32.7*	−40.8*
		(−0.045)	(−0.181)	(−0.091)	(−0.113)

Strain is the ± percent change in muscle length during the oscillatory length change cycle. Duty cycle is the duration of the burst of electromyographic activity during each oscillatory cycle expressed as a proportion of the oscillation period. Phase is the timing of the onset of the activity burst relative to the onset of shortening, expressed in degrees (one oscillation cycle = 360°). Negative values indicate muscle activity preceding muscle shortening. For comparison, phase expressed as a proportion of the period oscillation is provided in parentheses. Data are not provided for the ANT-1 position because the data set for that position at 2.5 BL s^{-1} is not complete. Sample size (n) is given in parentheses at the top of each column.

* Red muscle data from Rome *et al.* (1993); pink muscle data from Coughlin and Rome (1996).

studies report results similar to those presented here—a smaller phase shift for red muscle at more anterior positions. In a few fish, such as rainbow trout smolts (Williams *et al.*, 1989) and, at some swimming speeds, bass (Johnson *et al.*, 1994; Jayne and Lauder, 1995), a positive phase of red muscle activity has been reported for anterior positions. In these fish, muscle shortening occurs prior to muscle stimulation. In general, this was not observed in scup, although for a few fish, red muscle at the ANT-1 position did have a positive phase at low swimming speeds (unpubl. data). However, technical difficulties inherent in measurements of the muscle length change at this position lead to considerable uncertainty of the phase.

For rainbow trout, at least, a positive phase shift of muscle activation results in net negative power production (Coughlin and Burdick, 1996). Anterior muscle that undergoes either a very small negative phase shift or a positive phase shift will not contribute significantly to powering swimming (Rome *et al.*, 1993; Coughlin and Rome, 1996). For this reason, Hammond *et al.* (1998) suggest that the phase data from Williams *et al.* (1989) cannot reflect red muscle activity during steady swimming in trout. However, the many species of fish that show a relatively low negative phase in the anterior red muscle probably swim similarly to scup: most of the power is generated by the posterior musculature. Curiously, the data of Gillis (1998) suggest the same may be true for eels: at low steady swimming speeds, only the posterior red muscle is recruited to power swimming; the anteriormost red muscle is not recruited until the highest steady swimming speeds. Furthermore, when it is recruited, the negative phase shift is smaller than in posterior muscle (Gillis, 1998). This small negative phase shift may limit power production by anterior eel red muscle during swimming and, therefore, be associated with the lack of recruitment of this muscle at lower swimming speeds.

No previous research has reported on the relative phase differences in the stimulation of the aerobic muscle fibers of fish during each length change cycle of swimming. During each cycle of length change, pink muscle is stimulated after red muscle consistently (Fig. 4), except in the more anterior positions at lower swimming speeds. This correlates with the faster activation kinetics of pink muscle (Coughlin *et al.*, 1996): since it activates more rapidly, its stimulation can occur nearer to the onset of muscle shortening. Otherwise, it would reach high force levels while the muscle was still lengthening and might then generate net negative work during the length change cycle. Jayne and Lauder (1994) report similar results for red and white muscle in bass swimming at high, unsteady speeds. In those fish, white muscle stimulation lagged behind red muscle stimulation at a given longitudinal position. However, the lag between red and white activation was the same for both anterior and posterior positions; this finding differs from our results. We found that the phase difference between red and pink muscle increased at the more posterior positions of steady swimming scup.

Pink muscle function in swimming fish

Pink muscle is employed effectively by swimming scup. At maximal steady swimming speeds at both 10° and 20°C, pink muscle is heavily recruited and allows fish to swim steadily at speeds greater than possible with red muscle alone. At swimming speeds at which the performance of red muscle is near maximal, pink muscle produces considerable power for swimming (Coughlin and Rome, 1996). In addi-

tion, across a range of swimming speeds, the activation patterns of pink muscle (*i.e.* the delayed onset of activation) are well timed to take advantage of this muscle's faster rate of activation. At submaximal swimming speeds, the pink muscle at anterior body positions is a relatively ineffective source of power, and its recruitment is correspondingly limited.

Acknowledgments

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